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Salivary cortisol and pathogen disgust predict men's preferences for feminine shape cues in women's faces

Benedict C. Jones[a,*], Corey L. Fincher[a], Lisa L.M. Welling[b], Anthony C. Little[c], David R. Feinberg[d], Christopher D. Watkins[e], Emad A.S. Al-Dujaili[f], Lisa M. DeBruine[a]

[a] Institute of Neuroscience & Psychology, University of Glasgow, Scotland, UK
[b] Department of Psychology, Oakland University, MI, USA
[c] Department of Psychology, Neuroscience & Behaviour, McMaster University, Ontario, Canada
[d] School of Natural Sciences, University of Stirling, Scotland, UK
[e] School of Social and Health Sciences, University of Abertay, Scotland, UK
[f] Centre for Cardiovascular Science, The Queen's Medical Research Institute, Edinburgh, Scotland, UK

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ABSTRACT

Recent studies suggest that individuals who are particularly concerned about infectious diseases show stronger preferences for exaggerated sex-typical characteristics in potential mates' faces. However, these studies have generally investigated individual differences in *women's* mate preferences and relied on questionnaires to assess disease-related concerns. Here we show that men's scores on the pathogen disgust subscale of the Three Domains of Disgust Scale are positively correlated with their preferences for femininity in women's faces and that this relationship is independent of the possible effects of both sexual and moral disgust. We then show that men with higher trait (i.e., average) salivary cortisol, a biomarker for immunosuppression, have stronger preferences for femininity in women's faces. Finally, we show that pathogen disgust is correlated with partnered men's femininity ratings of both their actual and ideal romantic partner. Together, these findings suggest that disease-related factors are important for individual differences in men's mate preferences.

1. Introduction

Several lines of evidence suggest that exaggerated sex-typical facial characteristics (i.e., masculine characteristics in men's faces and feminine characteristics in women's faces) are positively correlated with indices of good health and dominance (reviewed in Little et al., 2011a; Puts et al., 2012). For example, individuals displaying more exaggerated sex-typical facial characteristics report fewer past health problems (e.g., Thornhill and Gangestad, 2006). Additionally, men with higher levels of testosterone, a correlate of men's facial masculinity in several studies (e.g., Penton-Voak and Chen, 2004; Roney et al., 2006), tend to possess more efficient immune systems (Rantala et al., 2012), while women with higher levels of estrogen, a correlate of facial femininity in women (Law Smith et al., 2006), tend to be in good physical health (e.g., van Anders, 2010). Consistent with these findings for measures of *actual* health, masculinized versions of men's faces are perceived to be healthier than feminized versions (e.g., Johnston et al., 2001; Scott et al., 2008; but see also Boothroyd et al., 2005) and feminized versions of women's faces are perceived to be healthier than masculinized versions (e.g., Johnston et al., 2001; Moore et al., 2011; Scott et al., 2008). Men displaying masculine facial characteristics are also physically stronger than their relatively feminine peers (Fink et al., 2007) and masculine men and women tend to be perceived as being physical stronger and more dominant than feminine men and women (e.g., Jones et al., 2010). Collectively, this work then suggests that exaggerated sex-typical facial characteristics are valid cues to men's and women's health and that masculine facial characteristics signal men's and women's dominance.

Although individuals displaying exaggerated sex-typical physical characteristics are preferred as mates in many non-human species (see, e.g., Clutton-Brock, 2009; Emlen, 2008 for reviews), the relationship between these characteristics and facial attractiveness in humans can be variable (reviewed in Little et al., 2011a). Concerns about infectious disease are one factor that may be important for this variability (DeBruine et al., 2010a; Tybur and Gangestad, 2011); individuals who are particularly concerned about infectious diseases may show stronger preferences for potential mates displaying exaggerated sex-typical characteristics due to the direct benefits (e.g., reduced risk of contracting illnesses) and/or indirect benefits (e.g., increased offspring health) thought to be associated with choosing a healthy mate (DeBruine et al., 2010a; Little

* Corresponding author. Tel.: +44 01411 330 5089.
E-mail address: ben.jones@glasgow.ac.uk (B.C. Jones).

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et al., 2011b; Tybur and Gangestad, 2011). Consistent with this proposal, women who report particularly strong disgust reactions to scenarios describing possible sources of pathogens, a measure hypothesized to reflect individual differences in vulnerability to disease (Tybur et al., 2009), also tend to show particularly strong preferences for masculine characteristics in men's faces (DeBruine et al., 2010a). Importantly, this relationship between pathogen disgust and women's masculinity preferences occurred independently of the possible effects of sexual or moral disgust, suggesting that it is not simply due to individual differences in general disgust sensitivity (DeBruine et al., 2010a). These findings have recently been replicated and extended to women's preferences for masculine characteristics in men's voices and bodies (Jones et al., in press). Other work has also found that women who rated their own health to be relatively poor showed particularly strong preferences for masculine characteristics in men's voices, at least when assessing men's attractiveness for hypothetical short-term relationships (Feinberg et al., 2012). While these findings suggest that women's vulnerability to disease may be positively correlated with individual differences in their preferences for masculine men (but see also Scott et al., 2008), other studies have suggested that measures of vulnerability to disease also predict population-level differences in women's masculinity preferences (DeBruine et al., 2010b, 2011, 2012a); women in geographic regions with poorer health (e.g., regions with higher pathogen loads or higher mortality rates due to communicable diseases) tend to show stronger preferences for masculine characteristics in men's faces (DeBruine et al., 2010b, 2011, 2012a; but see also Brooks et al., 2011). Consistent with interpretations of these findings that emphasize a potential causal effect of vulnerability to disease on mate preferences, priming concerns about pathogens increases both women's (Little et al., 2011b; Watkins et al., 2012) and men's (Little et al., 2011b) preferences for exaggerated sex-typical facial characteristics in potential mates.

The findings described above suggest that factors related to vulnerability to disease predict, and potentially directly influence, preferences for exaggerated sex-typical characteristics in potential mates' faces. However, prior work on this topic has generally focused on investigating variability in *women's* mate preferences. Although Little et al. (2011b) demonstrated that priming with pathogen cues increases men's preferences for feminine female faces, suggesting that variation in environmental cues to disease may influence men's mate preferences, it is still important to establish if naturally occurring differences in disease-related factors that occur *between* individuals also predict men's preferences for exaggerated sex-typical characteristics in women's faces. To address this issue, Study 1 and Study 2 investigated the relationship between individual differences in men's pathogen disgust and their preferences for feminized versus masculinized versions of women's faces. We assessed individual differences in pathogen, moral, and sexual disgust sensitivity using Tybur et al.'s (2009) Three Domains of Disgust Scale (*sensu* DeBruine et al., 2010a). Following DeBruine et al.'s (2010a) findings for disgust sensitivity and women's judgments of men's facial attractiveness, we predicted that men's pathogen disgust would be positively correlated with their preference for femininity in women's faces and that this relationship would be independent of the possible effects of men's moral or sexual disgust.

A further limitation of prior work on the relationship between disease-related factors and variation in mate preferences is the reliance on questionnaires to assess vulnerability to disease. Consequently, it is unclear if more objective measures of vulnerability to disease, such as biomarkers for immunosuppression, predict mate preferences in ways that are consistent with this prior work. To address this potentially important limitation, Study 3 investigated the relationship between men's trait (i.e., average) levels of salivary cortisol and their preference for feminized versus masculinized versions of women's faces. Cortisol plays an important, but complex, role in regulating the immune system (see Martin, 2009; Sapolsky et al., 2000 for comprehensive reviews). For example, the first wave of glucocorticoids produced in stress responses have both stimulating and inhibitory effects on immunity (Chrousos, 1995; Reichlin, 1993) and both infectious and noninfectious stressors can trigger immune activation (Harbuz and Lightman, 1992; Morrow et al., 1993). However, this activation is typically relatively short-lived (Sapolsky et al., 2000). Where levels of glucocorticoids are elevated for relatively long periods of time, however, such as days or even weeks, they tend to have immunosuppressive effects, such as inhibition of the synthesis, release, and efficacy of mediators that promote immune reactions (see Sapolsky et al., 2000; Martin, 2009). Since these latter results suggest that high trait (i.e., average) levels of salivary cortisol will likely be a biomarker for immunosuppression, we predicted that men with relatively high trait cortisol would show particularly strong preferences for feminine women.

In these three initial studies, we also investigated men's judgments of the attractiveness of feminized versus masculinized versions of *men's* faces. Given that Little et al. (2011b) demonstrated that priming men's concerns about pathogens altered their preferences for feminine women, but not feminine men, we predicted that neither pathogen disgust nor trait levels of cortisol would predict individual differences in men's preferences for feminized versus masculinized versions of men's faces.

Many researchers (e.g., Puts et al., 2012) have recently highlighted the importance of investigating whether factors that predict individual differences in attractiveness judgments of opposite-sex stimuli also predict individual differences in other measures of mate preferences, such as the characteristics of participants' actual romantic partners. Consequently, in Study 4 we investigated the relationship between partnered men's pathogen disgust and their femininity ratings of both their actual and ideal romantic partner. As in Studies 1 and 2, we predicted that men reporting higher levels of pathogen disgust would report both having more feminine actual partners and desiring more feminine ideal partners and that these relationships between pathogen disgust and femininity preferences would be independent of the possible effects of moral and sexual disgust.

2. Study 1

Study 1 investigated the relationships between men's preferences for feminized versus masculinized versions of faces and their scores on the pathogen, moral, and sexual disgust subscales of Tybur et al.'s (2009) Three Domains of Disgust Scale.

2.1. Methods

2.1.1. Participants

Sixty-three white heterosexual men (mean age = 23.16 years, SD = 4.70 years) participated in this laboratory-based study. All of these men were undergraduate students, postgraduate students, or staff at the University of Aberdeen.

2.1.2. Stimuli

The methods we used to manufacture stimuli to assess perceptions of the attractiveness of feminized versus masculinized versions of men's and women's faces have been used in many previous studies (e.g., DeBruine et al., 2006; Perrett et al., 1998; Welling et al., 2007, 2008). Responses to stimuli manufactured using these methods are known to be very similar to responses to stimuli manufactured using other methods for manipulating sexually dimorphic characteristics in face images (e.g., DeBruine et al., 2006, 2010c).

First, we manufactured a female prototype (i.e., average) face by using specialist software (Tiddeman et al., 2001) to average the shape, color, and texture information from images of 50 young white women's faces. A male prototype face was also manufactured in this way by averaging the shape, color, and texture information from images of 50 young white men's faces. The 100 individual face photographs (50 female and 50 male) were taken under standardized lighting conditions and against

a constant background. Individuals who posed for these photographs removed any facial jewelry or spectacles and adopted neutral expressions with direct gaze.

Next, we randomly selected 10 images from the set of 50 individual female faces and 10 images from the set of 50 individual male faces. We then created a feminized and a masculinized version of each of these 10 female and 10 male images by adding or subtracting 50% of the linear (i.e., vector) differences in 2D shape between symmetrized versions of the female and male prototypes to (or from) each individual image. This process created 20 pairs of face images in total (10 female pairs and 10 male pairs), with each pair consisting of a feminized and a masculinized version of one of the individual face images. Examples of these stimuli are shown in Fig. 1. Note that our feminized and masculinized versions of faces differed in sexually dimorphic shape characteristics only (i.e., were matched in other regards, such as identity, color, and texture, Tiddeman et al., 2001).

2.1.3. Manipulation check

We conducted an initial pilot study to check that the feminized and masculinized versions of female and male faces differed reliably in perceived femininity. The 20 pairs of face images (each pair consisting of a feminized and masculinized version of the same face) were presented to 20 men (mean age = 26.61 years, SD = 9.12 years), who were instructed to indicate which face in each pair looked more feminine. Trial order and the side of the screen on which any given image was presented were both fully randomized. We then used one-sample *t*-tests to compare the proportion of trials on which participants correctly identified the feminized face with what would be expected by chance alone (i.e., 0.5). These analyses confirmed that the feminized versions of faces were perceived to be more feminine than the masculinized versions of faces when judging women's ($t(19) = 13.37$, $p < .001$, $d = 3.00$, $M = .90$, SEM = .03) and men's ($t(19) = 13.48$, $p < .001$, $d = 3.02$, $M = .93$, SEM = .03) femininity. These findings are consistent with prior research showing that these methods for manipulating sexually dimorphic facial characteristics reliably alter perceptions of femininity-masculinity (e.g., DeBruine et al., 2006; Welling et al., 2007, 2008).

2.1.4. Three Domains of Disgust Scale (TDDS)

This 21-item measure, developed by Tybur et al. (2009) and previously used to explore the relationship between different aspects of disgust sensitivity and women's face preferences (DeBruine et al., 2010a), asks participants to rate each of 21 actions using a 7-point scale (0 = not at all disgusting, 6 = extremely disgusting). The actions are divided into three domains: moral disgust (e.g., deceiving a friend), sexual disgust (e.g., hearing two strangers having sex), and pathogen disgust (e.g., stepping on dog poop). The order of questions is randomized between participants. The TDDS has good internal and external validity (Tybur et al., 2009).

2.1.5. Procedure

Men were shown the 20 pairs of faces (each pair consisting of feminized and masculinized versions of the same individual) and were asked to choose the face in each pair that was more attractive. Pairs of faces were presented in a fully randomized order and the side of the screen on which any given image was shown was also randomized. This method for assessing men's preferences for feminized versus masculinized versions of faces has been used in many previous studies (e.g., Jones et al., 2007; Little et al., 2011b; Welling et al., 2008). Recent work also suggests that this method produces femininity preference scores for judgments of women's faces that are positively correlated with the facial femininity of men's actual partners (DeBruine et al., 2012b) and that are similar to those obtained via attractiveness ratings of individual face images (Rhodes, 2006). Each participant also completed Tybur et al.'s (2009) TDDS. The order in which participants completed the TDDS and face preference test was fully randomized.

2.1.6. Initial processing of data

For each participant, we calculated the proportion of trials on which he chose feminized versions of women's faces as more attractive than masculinized versions and, separately, the proportion of trials on which he chose feminized versions of men's faces as more attractive than masculinized versions. We also calculated men's scores on the pathogen ($M = 22.38$, SD = 7.58), sexual ($M = 11.49$, SD = 6.63), and moral ($M = 29.87$, SD = 7.22) disgust subscales of the TDDS, following the procedure described by Tybur et al. (2009).

2.2. Results

A one-sample *t*-test comparing the proportion of trials on which men judged feminized versions of women's faces to be more attractive than masculinized versions with what would be expected by chance alone (i.e., 0.5) demonstrated that men chose the feminized versions significantly more often than would be expected by chance ($t(62) = 9.57$, $p < .001$, $d = 1.21$, $M = .75$, SEM = .03). A corresponding *t*-test for judgments of men's faces demonstrated that men chose masculinized versions of men's faces more often than would be expected by chance ($t(62) = -3.91$, $p < .001$, $d = 0.49$, $M = .40$, SEM = .03).

Next, we analyzed men's judgments of *women's* faces using a regression analysis in which the proportion of trials on which men judged feminized versions of women's faces to be more attractive than masculinized versions was entered as the dependent variable and men's scores on the pathogen, moral, and sexual disgust subscales of the TDDS were entered as separate predictors. This analysis revealed the predicted significant positive correlation between men's scores on the pathogen disgust subscale and their preferences for feminized versions of women's faces ($t = 2.35$, standardized beta = .32, $p = .022$). Men's scores on the moral disgust subscale and their preferences for feminized versions of women's faces were negatively correlated ($t = -2.57$, standardized beta = −.35, $p = .013$). Men's scores on the sexual disgust subscale did not predict their preferences for feminized versions of women's faces ($t = 0.39$, standardized beta = .05, $p = .69$). Repeating this analysis with participant age as an additional predictor did not alter this pattern of significant results.

Finally, we analyzed men's judgments of *men's* faces in the same way. Men's scores on the pathogen disgust subscale did not predict their preference for feminized versions of men's faces ($t = 0.77$, standardized beta = .11, $p = .45$). Men's scores on the moral disgust subscale tended to be negatively correlated with their preference for feminized versions of men's faces, though this relationship was not significant ($t = -1.67$, standardized beta = −.23, $p = .099$). Men's scores on the sexual disgust subscale tended to be positively related to their preference for feminized versions of men's faces, though this relationship was also not significant ($t = 1.84$, standardized beta = .25, $p = .071$). Repeating this analysis with participant age included as an additional predictor did not alter the pattern of results.

3. Study 2

Like Study 1, Study 2 investigated the relationships between men's preferences for feminized versus masculinized versions of faces and their scores on the three subscales of Tybur et al.'s (2009) TDDS. Study 2 explored these relationships using both a different sample of male participants and a different set of face stimuli from those used in Study 1 in order to test the generalizability of Study 1's findings.

3.1. Methods

3.1.1. Participants

One hundred and four heterosexual men (mean age = 24.27 years, SD = 5.59 years) took part in this study. The study was run online, with participants recruited from links posted on social bookmarking websites (e.g., stumbleupon.com). Prior research has demonstrated that men's responses to feminized versus masculinized versions of faces in laboratory and online tests are very similar indeed (e.g., Jones et al., 2007).

3.1.2. Face stimuli

The methods we used to manufacture face stimuli were the same as those used in Study 1, except that (1) the male and female prototypes used to define the sexual dimorphism continuum along which individual faces were transformed were manufactured from 20 individual white male faces and 20 individual white female faces, respectively, and (2) feminized and masculinized versions of each of these 40 individual faces (20 female and 20 male) were manufactured for use in the face preference tests. None of the face images used in Study 2 had been used in Study 1.

3.1.3. Manipulation check

The 40 pairs of face images (each pair consisting of a feminized and masculinized version of the same face) were presented to 20 men (mean age = 22.62 years, SD = 3.51 years), who were instructed to indicate which face in each pair looked more feminine using the same procedure as the *Manipulation check* in Study 1. Consistent with findings from both Study 1's *Manipulation check* and prior research (e.g., DeBruine et al., 2006; Welling et al., 2007, 2008), one-sample *t*-tests confirmed that the feminized versions of faces were perceived to be more feminine than the masculinized versions of faces when judging women's ($t(19) = 17.09$, $p < .001$, $d = 3.90$, $M = .89$, SEM = .02) and men's ($t(19) = 14.70$, $p < .001$, $d = 3.31$, $M = .93$, SEM = .03)

Fig. 1. Examples of masculinized (left) and feminized (right) male face images.

femininity. None of the men who took part in this pilot study had taken part in any of the other studies.

3.1.4. Procedure

Participants completed a face preference test that was identical to the one used in Study 1, except that the stimuli were the 40 pairs of face images (20 male and 20 female) described above. They also completed the TDDS (Tybur et al., 2009). As in Study 1, the order in which men completed the TDDS and face preference was randomized across participants.

3.1.5. Initial processing of data

As in Study 1, we calculated the proportion of trials on which each participant chose feminized versions of women's faces as more attractive than masculinized versions. Corresponding scores were calculated for judgments of men's faces. We also calculated men's scores on the pathogen ($M = 23.71$, SD = 7.25), sexual ($M = 12.04$, SD = 7.59), and moral ($M = 25.73$, SD = 9.56) disgust subscales of the TDDS.

3.2. Results

Data in Study 2 were analyzed in the same way as in Study 1. One-sample t-tests showed that men were significantly more likely to choose feminine women's faces than masculine women's faces ($t(103) = 20.47$, $p < .001$, $d = 2.00$, $M = .83$, SEM = .02). By contrast, feminine men's faces were not chosen as the more attractive significantly more often than masculine men's faces ($t(104) = 1.34$, $p = .18$, $d = 0.13$, $M = .54$, SEM = .03). For judgments of women's faces, pathogen disgust ($t = 2.27$, standardized beta = .24, $p = .025$), but not moral disgust ($t = -0.98$, standardized beta = −.10, $p = .33$) or sexual disgust ($t = -1.55$, standardized beta = −.16, $p = .12$), predicted men's femininity preferences. For judgments of men's faces, neither pathogen disgust ($t = -0.02$, standardized beta = .00, $p = .98$), moral disgust ($t = 0.12$, standardized beta = .01, $p = .91$), nor sexual disgust ($t = 0.60$, standardized beta = .07, $p = .55$), predicted men's femininity preferences. Repeating the regression analyses with participant age included as an additional predictor did not alter these patterns of results.

4. Study 3

Study 3 investigated the relationship between men's preferences for feminized versus masculinized versions of faces and their trait (i.e., average) salivary cortisol levels.

4.1. Methods

4.1.1. Participants

Twenty-nine white, heterosexual men (mean age = 20.48 years, SD = 3.56 years) took part in the study. All participants were undergraduate students at the University of Aberdeen, participating in the study for course credit.

4.1.2. Procedure

Each participant was tested on two occasions, with the second test session taking place 2 weeks after the first test session. All testing took place between 10 am and 3 pm. The time of testing was held constant within participants (i.e., both test sessions took place at the same time of day). In each test session, participants completed a face preference test that was identical to the one used in Study 2 (i.e., both the procedure and the face stimuli were the same as those in Study 2). In each test session, participants also deposited between 3 and 5 mL of saliva by spitting directly into plastic pharmaceutical vials at the beginning of the session. The vials were then sealed and frozen at −20 °C until analysis. We did not use chewing gum to stimulate saliva and none of our participants reported having consumed alcohol or undertaken strenuous exercise in the previous 24 h. All of our participants indicated that they were not currently using any form of medication.

In the first test session, 27 of the participants also completed the trait anxiety subscale of the State Trait Anxiety Inventory (Spielberger, 1968/1977). Note that two of the participants opted not to complete this anxiety questionnaire. These anxiety data were collected so that we could control for the possible effects of trait anxiety on face preferences (e.g., Conway et al., 2008).

4.1.3. Cortisol assay methodology

Salivary cortisol levels were determined by the Cardiovascular Centre Laboratories (Queen's Medical Research Institute, Edinburgh) using an in-house ELISA method (Al-Dujaili et al., 2011; Al-Dujaili and Ashmore, 2007). Briefly, saliva samples were first extracted with diethylether and the re-constituted samples were then pipetted into the 96-well pre-coated ELISA plate. Increasing doses of cortisol standards and quality controls were included and the plate incubated with anti-cortisol antibody for 2 h at room temperature. Following the addition of the enzyme tracer and further incubation for 1 h, the plate was developed and read using MRX ELISA reader. Cross-reactivity with most interfering steroids was minimal except for deoxy-cortisol (1%) and cortisone (0.75%). Assay sensitivity was 0.14 nmol/L. Intra-assay and inter-assay imprecision were 4.6% and 6.8% respectively. Recovery results for cortisol levels of 2.4–40.8 nmol/L were 95.8–106.7%. Additional analyses of cortisol levels in a subset of the saliva samples using Salimetrics ELISA showed that cortisol measures obtained using our in-house ELISA method are highly correlated with those obtained using Salimetrics ELISA ($R^2 = 0.96$). A strong correlation between cortisol measures obtained using our in-house ELISA method and those obtained using Salimetrics ELISA has also been reported in other samples (e.g., Conway et al., 2007).

4.1.4. Initial processing of data

For each participant, we identified the test sessions with the highest and lowest salivary cortisol levels. Salivary cortisol was significantly higher

($t(28) = 6.26$, $p < .001$, $d = 1.16$) in the high cortisol test session (mean = 13.60 nmol/L, SD = 7.72 nmol/L) than in the low cortisol test session (mean = 7.33 nmol/L, SD = 4.66 nmol/L). Allocating test sessions to high and low cortisol test sessions did not confound cortisol level and order of testing; the first test session was the high cortisol test session for 16 of the 29 participants, which is not significantly different to what would be expected by chance alone (Binomial test: $p = .71$).

For each participant, we calculated the proportion of trials (out of 20) on which feminine versions of faces were chosen as more attractive than masculine versions. This femininity preference score was calculated separately for female and male faces. We calculated corresponding values for the high and low cortisol test sessions separately. Thus, each participant provided four femininity preference scores for each of (1) male faces in the high cortisol test session, (2) female faces in the high cortisol test session, (3) male faces in the low cortisol test session, and (4) female faces in the low cortisol test session.

4.2. Results

First, we used one-sample *t*-tests to compare the proportion of trials on which feminine faces were chosen as the more attractive with what would be expected by chance alone (i.e., 0.5). These one-sample *t*-tests showed that men were significantly more likely to choose feminine women's faces than masculine women's faces in both the high cortisol test session ($t(28) = 5.22$, $p < .001$, $d = 0.97$, $M = .68$, SEM = .03) and low cortisol test session ($t(28) = 6.78$, $p < .001$, $d = 1.26$, $M = .69$, SEM = .03). By contrast, feminine male faces were not chosen as the more attractive significantly more often than masculine male faces in either the high cortisol test session ($t(28) = 1.46$, $p = .16$, $d = 0.26$, $M = .55$, SEM = .03) or low cortisol test session ($t(28) = 1.80$, $p = .08$, $d = 0.33$, $M = .57$, SEM = .04).

Next, we analyzed femininity preference scores using a repeated measures ANOVA with the factors *test session* (high cortisol, low cortisol) and *sex of face judged* (male, female). This analysis revealed a significant main effect of *sex of face judged* ($F(1,28) = 17.19$, $p < .001$, partial eta^2 = .38), whereby men were more likely to choose feminized faces when judging women's attractiveness than when judging men's attractiveness (female faces: $M = 0.68$, SEM = 0.03; male faces: $M = 0.56$, SEM = 0.03). There were no other significant effects (both $F < 0.32$, both $p > .58$, both partial eta^2 < .012).

Salivary cortisol levels were positively correlated between high and low cortisol test sessions ($r = .73$, $N = 29$, $p < .001$), as were preferences for femininity in women's faces ($r = .38$, $N = 29$, $p = .043$) and preferences for femininity in men's faces ($r = .54$, $N = 29$, $p = .002$). In light of these correlations, and because the repeated measures ANOVA described above revealed no significant within-subject effects of high versus low cortisol, we calculated each participant's average (i.e., trait) cortisol level ($M = 10.46$ nmol/L, SD = 5.78 nmol/L) and femininity preference scores (female faces: $M = 0.68$, SD = 0.14; men's faces: $M = 0.56$, SD = 0.17) by averaging values across the two test sessions. Previous studies have averaged cortisol measures across multiple samples in this way in order to get a more reliable measure of trait (i.e., average) hormone levels (e.g., Rantala et al., 2012). We then conducted a regression analysis with average cortisol level as the dependent variable and average preference for femininity in men's and women's faces as predictors. As we had predicted, preference for femininity in women's faces and average cortisol were positively correlated ($t = 2.55$, standardized beta = .51, $p = .017$). Although men with particularly weak preferences for femininity in men's faces tended to have higher average cortisol levels, this relationship was not significant ($t = -1.79$, standardized beta = −.36, $p = .085$). Including trait anxiety scores as an additional predictor also revealed a positive relationship between preference for femininity in women's faces and average cortisol level ($t = 2.42$, standardized beta = .50, $p = .024$). Men with particularly weak preferences for femininity in men's faces also tended to have higher average cortisol levels in this additional analysis, although this relationship was also not significant ($t = -1.93$, standardized beta = −.39, $p = .067$). The positive relationship between men's trait anxiety and average cortisol was not significant ($t = 1.01$, standardized beta = .18, $p = .32$). Including men's own age as an additional predictor in these regression analyses did not alter the patterns of results.

5. Study 4

The previous studies suggest that men's preferences for feminine shape characteristics in women's faces are positively correlated with both pathogen disgust and average cortisol levels, raising the possibility that these factors might also be correlated with men's mate choices. Indeed, many researchers have recently emphasized the importance of investigating whether individual differences observed in preferences for facial characteristics extend to measures of actual mate choice (e.g., Puts et al., 2012). Consequently, in Study 4 we investigated the relationships between partnered men's responses on the TDDS and their ratings of the femininity of both their actual and ideal romantic partner.

5.1. Methods

Six hundred and fourteen heterosexual men (mean age = 25.67 years, SD = 6.01 years) who reported that they currently had a romantic partner ('partnered men') and 769 heterosexual men (mean age = 22.92 years, SD = 4.56 years) who reported that they did not currently have a romantic partner ('unpartnered men') took part in this online study.

All participants completed the TDDS (Tybur et al., 2009) and were asked to rate the femininity of their ideal romantic partner. Partnered men were also asked to rate the femininity of their actual romantic partner. Femininity ratings were made using a seven-point scale on which high scores indicated greater femininity. This method has previously been used to demonstrate that masculinity ratings of women's actual and ideal partners are positively correlated with their preferences for masculine characteristics in men's face images (DeBruine et al., 2006). We calculated partnered men's scores on the pathogen ($M = 23.93$, SD = 7.22), sexual ($M = 10.87$, SD = 7.20), and moral ($M = 26.66$, SD = 8.79) disgust subscales of the TDDS. We also calculated unpartnered men's scores on the pathogen ($M = 23.15$, SD = 7.05), sexual ($M = 12.34$, SD = 8.09), and moral ($M = 26.10$, SD = 8.78) disgust subscales of the TDDS.

5.2. Results

A regression analysis in which partnered men's femininity ratings of their actual romantic partner were entered as the dependent variable and pathogen, moral, and sexual disgust were entered as separate predictors revealed a positive relationship between pathogen disgust and femininity ratings ($t = 2.47$, standardized beta = .10, $p = .014$) and no other significant associations (both absolute $t < 0.17$, both absolute standardized beta < .013, both $p > .76$). Repeating this analysis with partnered men's femininity ratings of their ideal, rather than actual, romantic partner as the dependent variable also revealed a positive relationship between pathogen disgust and femininity ratings ($t = 3.38$, standardized beta = .14, $p < .001$) and no other significant associations (both absolute $t < 1.18$, both absolute standardized beta < .05, both $p > .23$). Including men's age as an additional predictor in these analyses did not alter the patterns of results.

A regression analysis in which unpartnered men's femininity ratings of their ideal romantic partner were entered as the dependent variable and pathogen, moral, and sexual disgust were entered as separate predictors revealed a positive relationship between pathogen disgust and femininity ratings ($t = 2.64$, standardized beta = .10, $p = .009$) and no other significant associations (both absolute $t < 1.19$, both absolute standardized beta < .046, both $p > .23$). Again, including men's age as an additional predictor in this analysis did not alter the pattern of results.

6. Discussion

In Studies 1–3, men generally preferred feminized versions of women's faces to masculinized versions, which is consistent with previous work (for a meta-analytic review see Rhodes, 2006).

However, each of these studies also revealed systematic variation (i.e., individual differences) in the strength of men's preferences for femininity in women's faces. Importantly, the nature of these individual differences suggests that disease-related factors predict, and potentially influence, variation in men's mate preferences. Moreover, Study 4's results suggest that the correlation between pathogen disgust and men's preferences for feminine women may also extend to their mate choices; partnered men with higher pathogen disgust reported having particularly feminine romantic partners.

In Study 1 and Study 2, men's pathogen disgust was positively correlated with their preference for feminine characteristics in women's faces. Moreover, these relationships were independent of the possible effects of both sexual and moral disgust, demonstrating that they are not due to individual differences in men's general disgust sensitivity. These findings parallel those reported in previous work on individual differences in women's mate preferences, in which women's pathogen disgust, independent of sexual or moral disgust, was positively correlated with their preference for exaggerated sex-typical characteristics in men's faces (DeBruine et al., 2010a; Jones et al., in press), voices, and body shapes (Jones et al., in press). Since exaggerated sex-typical characteristics in men's and women's faces appear to function, at least partly, as health cues (see Section 1), these findings suggest that individuals who show stronger aversions to potential sources of contagion also tend to place greater value in the health of potential mates. Thus, the individual differences observed in Study 1, Study 2, and prior work on the role of pathogen disgust in women's masculinity preferences (DeBruine et al., 2010a) may reflect the direct benefits (e.g., reduced risk of contracting illnesses) and/or indirect benefits (e.g., increased offspring health) thought to be associated with choosing a healthy mate (DeBruine et al., 2010a; Tybur and Gangestad, 2011). That pathogen disgust here predicted men's preferences for femininity in women's, but not men's, faces is also consistent with the results of a recent priming experiment in which priming men's concerns about pathogens increased their preference for femininity in women's, but not men's, faces (Little et al., 2011b). Unexpectedly, men's moral disgust was negatively correlated with their preference for feminized female faces. This finding was not predicted and was not replicated in Study 2 (although the direction of the correlation between moral disgust and femininity preference was also negative in Study 2). We do not draw any firm conclusions about this possible link between moral disgust and mate preferences other than to note that moral disgust may be an interesting avenue for future research on men's judgments of women's attractiveness.

In Study 3, men's preferences for feminine characteristics in women's faces were positively correlated with their own trait (i.e., average) salivary cortisol levels. Since trait (i.e., average) cortisol levels are likely to be a biomarker for immunosuppression (see Section 1), Study 3's findings extend those from Study 1 and Study 2 by showing that an objective index of vulnerability to disease (i.e., a biomarker for immunosuppression) also predicts men's preferences for feminine women. Importantly, we also show that this correlation between trait cortisol and men's femininity preferences is not due to individual differences in trait anxiety levels, which may also predict preferences for some facial characteristics (see, e.g., Conway et al., 2008). It is also unlikely to be due to other factors that are thought to contribute to variation in men's mate preferences, such as individual differences in testosterone levels (Welling et al., 2008) or attractiveness (Burriss et al., 2011; Jones et al., 2007), since these factors are not correlated with men's cortisol levels (Rantala et al., 2012). Importantly, while men's *trait* (i.e., average) cortisol levels predicted their femininity preferences in Study 3, the repeated measures ANOVA we conducted demonstrated that within-subject (i.e., state) changes in cortisol levels were not associated with a change in men's femininity preferences. Since short-term increases in cortisol do not necessarily have an immunosuppressive effect (Martin, 2009; Sapolsky et al., 2000) and, in some circumstances, can increase immune function (Martin, 2009; Sapolsky et al., 2000), this null finding for *state* cortisol levels is consistent with an interpretation of Study 3's findings that emphasizes the immunosuppressive properties of trait cortisol. Given the important role that glucocorticoids play in regulating the immune system (Martin, 2009; Sapolsky et al., 2000), our findings may even suggest cortisol as a candidate proximate mechanism for pathogen-related individual differences in men's mate preferences. This is potentially noteworthy, since most research into the potential hormonal mechanisms for individual differences in human mate preferences has focused on the possible effects of sex hormones (e.g., Jones et al., 2005; Puts, 2006; Welling et al., 2007, 2008; Garver-Apgar et al., 2008). Experiments testing for a causal effect of glucocorticoids on human mate preferences may shed further light on this possibility.

The weak (i.e., non-significant, $p = .085$) negative correlation between men's trait cortisol and their preference for feminine men (Study 3) suggests that men with high trait cortisol potentially prefer more masculine men. This unexpected relationship was independent of the relationship between trait cortisol and men's preferences for feminine women, suggesting that it may not necessarily arise from individual differences in men's vulnerability to disease. Consistent with this suggestion, Little et al. (2011b) found that priming men's concerns about pathogens increased their preference for femininity in women's, but not men's, faces (see Study 1 and Study 2 for further evidence of this sex-specificity). A possible explanation for the unexpected correlation between cortisol and judgments of men's facial attractiveness is that low-dominance men (i.e., men with relatively high trait levels of cortisol, reviewed in Cummins, 2006) look to offset the potential consequences of their low dominance (e.g., loss of resources) by allying themselves with masculine (i.e., dominant, Puts, 2010) men. Indeed, recent work suggests that cues of men's dominance are more salient to low-dominance men than they are to relatively high-dominance men (Watkins et al., 2010a,b) and that men form alliances, at least in part, to increase their safety and resource holding potential (e.g., von Rueden et al., 2011). Alternatively, since the correlation between trait cortisol and judgments of other men's attractiveness was not significant, the tendency for men with higher cortisol levels to report stronger preferences for masculine men may not be robust.

There has been considerable debate in the human attractiveness literature about the nature of the information signaled by feminine characteristics in women's faces, with researchers variously suggesting that men's preferences for feminine women reflect preferences for youth, maternal tendencies, health, and/or social status (see Moore et al., 2011 for a review of this literature). Our findings linking both men's concerns about infectious disease and an objective measure of their vulnerability to disease to their femininity preferences suggest that preferences for health cues do play a potentially important role in men's preferences for feminine characteristics in women's faces, complementing other work that has arrived at similar conclusions (Moore et al., 2011; Rhodes et al., 2007). However, we note here that while our data implicate health-related factors in men's femininity preferences, they certainly do not rule out the possibility that feminine facial characteristics also convey other potentially important information about women's mate qualities. Indeed, Rhodes et al. (2007) have shown that perceptions of women's health contribute to the relationship between women's facial femininity and attractiveness but do not necessarily fully explain it.

In conclusion, our studies show that both pathogen disgust (Studies 1 and 2) and trait cortisol levels (Study 3) are positively correlated with men's preferences for feminized versus masculinized

versions of women's faces. These data then suggest that individual differences in disease-related factors figure in men's mate preferences and complement previous work on individual differences in women's preferences for exaggerated sex-typical characteristics in potential mates' faces. Importantly, our results include the first demonstration of a link between vulnerability to disease and mate preferences using a biomarker of immunosuppression (trait, or average, cortisol). Stronger preferences for women displaying putative health cues among men who are particularly vulnerable to disease may reflect a compensatory strategy that evolved to help such men avoid infectious diseases and to maximize their reproductive fitness by increasing the health of their offspring. Indeed, consistent with the proposal that individual differences in men's pathogen disgust may contribute to their actual mate choices, we found that pathogen disgust was positively correlated with partnered men's ratings of the femininity of their current romantic partner (Study 4).

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